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RHINOCEROSES FROM THE THOMAS FARM MIOCENE OF FLORIDA

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INTRODUCTION

As long ago as 1941, Dr. Thomas Barbour invited me to study the two forms of rhinoceroses from the Thomas Farm quarry, Gilchrist County, Florida, in the collections of the Museum of Comparative Zoology. I am indebted to the late Dr. Barbour, then Director of the Museum of Comparative Zoology and to Dr. Theodore E. White for the opportunity to describe these forms; to Prof. Bryan Patterson, Dr. A. S. Romer, Mr. Henry Seton, Dr. Donald Baird and my other Harvard friends for hospitable assistance in studying this material. It is appropriate to mention the extended patience during the delay of the completion of this paper. The study was aided by the American Philosophical Society in Philadelphia, and the Rutgers Research Council. The drawings are by Mr. Eugene N. Fischer, supplemented by later ones in 1954 to 1961 by Dr. Florence D. Wood, following additional preparation and the discovery of new material. The preparation and preservation of this fragile material was done by Mr. Russell Olsen.

The abbreviations M.C.Z. and A.M.N.H. refer to the Museum of Comparative Zoology and the American Museum of Natural History, respectively. AP is anteroposterior, Tr is transverse, and e is estimated figure. Measurements throughout the paper are given in millimeters.

White described the geology and the fauna of the Thomas Farm quarry in 1942 (for its history see White, 1942, pp.3-4, and references cited therein), with the exception of the rhinoceros material. He determined the local fauna as early Arikareean or earliest Miocene. Previously, it had been considered early Hemingfordian which is "early middle Miocene" in age (Wood *et al.*, 1941). There is no association in the specimens taken from this quarry and none is established for the rhinoceros collection. However, the rhinoceroses fall into two clearly defined species of the Caenopinae. These two, one a very large animal, the other a small

one, are roughly comparable in size to the living black rhinoceros and to *Diceratherium cooki*, respectively. They are so distinctive that anything recognizable as rhinoceros bone or tooth can be allocated between the two. Both are new species and the larger is a new genus.

SYSTEMATIC DESCRIPTIONS

Order PERISSODACTYLA

Family RHINOCEROTIDAE Gray, 1821

Subfamily CAENOPINAE Breuning, 1922

FLORIDACERAS[1] new genus

Type species: F. whitei, new species.

Diagnosis: very large, long-legged, hornless rhinoceros, with small, complete and functional fifth digit in the manus; teeth intermediate in evolutionary progressiveness between *Diceratherium armatum* and *Aphelops*, but without close relationship to either line.

FLORIDACERAS WHITEI[2] new species

Type: M. C. Z. No. 4046, a damaged skull with left P^2-M^3 and right P^3-M^3; *paratype:* M.C.Z. No. 4435, a left mandibular ramus.

Hypodigm: Type and paratype and M.C.Z. Nos. 4047-4053, 7467-7556, including other, less complete skulls and mandibles, most of the girdles and limb bones, and representative parts of the axial skeleton.

Horizon and locality: Thomas Farm local fauna, late Arikareean, eight miles north of Bell, Gilchrist County, Florida.

Diagnosis: a relatively primitive true rhinoceros, but enormous for New World early Miocene age, almost the size of the living black rhinoceros; the skull is hornless and primitive, constricted behind postorbital processes of frontals, with a well developed sagittal crest; occiput deep, not markedly broad; postglenoid process fairly prominent, but much shorter than paroccipital process, which is long spike; dental formula: $I_1^?$ $C_0^{0?}$ dP_3^3 P_{4-3}^4 M_3^3; cheek teeth generally primitive, with ectolophs of upper cheek

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[1] *Florida*, the place of discovery, and *aceras*, without horn.

[2] The specific name acknowledges my indebtedness to Dr. Theodore E. White for his considerable collection from a critical age and region.

teeth more hypsodont than *Diceratherium armatum;* crochets on upper cheek teeth incipient to full size; I_2 large; a small but functional fifth digit in the manus.

DISCUSSION

The late Dr. H. G. Stehlin in the summer of 1927 called my attention to the problem of how to designate the first upper and lower premolars in rhinoceroses. In his opinion there is no replacement of this tooth in rhinoceroses or, for that matter, in perissodactyls in general. When asked if he considered it to belong to the deciduous or to the permanent series, he replied that it was apparently sometimes one, sometimes the other.

Since this hint, my observations on rhinocerotoids have led to the following generalizations:

1.   There is no evidence of replacement where the first premolar is concerned.
2.   The enamel is heavy as in permanent teeth, unlike the thin enamel of milk teeth.
3.   The first upper and lower premolars erupt with the deciduous series, after the second and third, and usually before the fourth deciduous premolar. The first upper premolar continues in use with the permanent series until old age, both in ancestral forms and in later forms which retain reasonably primitive dentitions. The first lower premolar erupts in the same sequence, but continues in function with the permanent series in some primitive forms only; more typically, it is lost with the deciduous series. There is also more individual variation as to the length of time it remains in service than for the upper tooth.

These general inferences apply specifically to *F. whitei* and the teeth in question are regarded as precociously erupting members of the permanent series, and as such are called P_1^1.

Floridaceras whitei has an interesting and contradictory combination of characters. The teeth are entirely too primitive for *Aphelops,* being only slightly more progressive than the *Diceratherium armatum* stage, but having a parallel character of an *Aphelops*-like crochet, incipient on P^3 and increasing to full development on M^2. In becoming more progressive or specialized, rhinoceros molars may increase the cutting surfaces of the fundamental loph pattern in a limited number of ways: by adding crochets, antecrochets and cristae, and by adding corrugations to these in turn. This often results in similar types of parallel

dental evolution in groups not closely related. The dentition of the type skull is nearly complete and unbroken but the skull proper is so badly crushed and fragmentary it is not subject to thorough interpretation. In preparation it had been disassembled and re-modelled with generous plaster after an *Aphelops* skull, which misleads the observer.

The most astonishing among the numerous primitive characters is the retention of a tetradactyl manus. Previously, *Trigonias* of the lower Oligocene was the latest American true rhinoceros known to have a fifth digit. Among Old World rhinoceroses, the entire *Aceratherium* line has a tetradactyl manus, including its last known representative, *A. incisivum* of the Pliocene. However, it should be pointed out that at least two American forms, of which the manus is unknown, *Amphicaenopus platycephalus* and *Subhyracodon kewi*, are merely presumed to be tridactyl.

DENTITION

In the type dentition of *Floridaceras whitei*, M.C.Z. No. 4046, the cheek teeth only are preserved (Pl. I, fig. 1). The first premolar is double rooted; P^2 is three rooted, the protoloph and metaloph are partly convergent and confluent 11.5 mm. above the complete internal cingulum; P^3 and P^4 are fully molariform in structure, although premolariform in outline. Crochets: bare trace on P^2, small on P^3 and P^4, large but not enormous on M^2, but nowhere as big as any on an *Aphelops* molar; cristae are absent; there is no antecrochet on P^{2-3}, a barely noticeable one on P^4, and there is a moderate swelling on M^{1-2}, less again on M^3; cingula are interrupted internally by the protocones of P^4-M^3. The internal cingulum is complete on P^2; attenuated on the protocone on P^3; in P^3 and P^4 it is strong across the valley and rises to a broad swell opposite the anterior slope of the metaloph; interrupted by the protocone, and barely by the hypocone of P^4; seems present across the valleys of M^{1-2}, weaker across valleys of M^3, not on inner ends of lophs, though there is a very faint suggestion of where it should be.

A partial skull, M.C.Z. No. 4048, very badly crushed, referred to *F. whitei*, is of interest chiefly because right P^{1-4} are present. The restoration of P^1 in the type illustration is from this specimen. P^1 has a well developed metaloph, a protoloph represented only by the crista-like ridge, and a strong low internal cingulum, except around the metaloph, where it is attenuated. A measurement across the occipital condyles, estimated at 148 mm. may be more reliable than that of the type.

The back of a cranium, M.C.Z. No. 4049, referred to *F. whitei,* is crushed, but this specimen is of particular interest since it confirms unmistakably the existence of a real sagittal crest. The crest, as such, extends 165.0 mm. anteriorly from the posterior edge of the center of the lambdoidal crest., i.e., ahead of the occipital surface, before it merges into the smooth brain case.

A crushed face and palate, with well worn teeth, M.C.Z. No. 4047, referred to *F. whitei,* is an older individual than the type. The dentition agrees in essential characters so far as these are not removed by wear, but gives no additional data. The nasals taper off gradually forward and end in a common stubby triangle. The nasal incision extends from the tip of the nasals to a point just above the border of the alveoli between P^2 and P^3, and measures 156.0 mm. in length. The roof of the nasals is partly imbedded in plaster, but as would be expected, there is no evidence of nasal rugosities.

A well-preserved, nearly complete left mandible (Pl. I, figs. 2, 3), M.C.Z. No. 4435, designated as the paratype, has I_2, P_{1-4} (of which P_1 is merely an alveolus), and M_{1-3}. The proportions of the jaw are long and slender, simple and unmodified. The jaw in general and the cheek teeth in particular are strikingly suggestive of *Diceratherium armatum.* The teeth, slightly worn, are relatively simple and unmodified. They are moderately high crowned, being approximately half the depth of the ramus. I_2, not fully erupted, is a large tooth, bluntly triangular in cross section, with a slight upturned flange on the median edge. Its enamel is very heavy laterally and ventrally, but very thin dorsally. The tip is slightly beveled medially with wear. The tooth has been compressed toward the symphysis so that if there had been a very small I_1 or an alveolus it has been destroyed. P_1 is indicated by a single-rooted open alveolus. P_2 has slight cingula on the anterior and posterior ends. Its pattern is simplified secondarily. The trigonid consists largely of the protoconid on which the paraconid forms a good-sized anterior flange, and the metaconid a smaller posterointernal extension. The talonid forms a continual crest from the metaconid region around a centrally enclosed pit. The third and fourth premolars are fully molariform but shorter proportionately, anteroposteriorly, than molars. The third lower premolar has weak cingula on the anterior and posterior ends. An internal extension partly blocks the valley out of the trigonid, but with a slight interruption at the opening

of the valley. The fourth lower premolar has cingula on the anterior and posterior ends. The anterior cingulum extends internally to the valley of the trigonid. An internal cingulum crosses the talonid valley. M_1 has slight cingula on the anterior and posterior ends. The anterior cingulum continues internally and stops just beyond the trigonid valley, with a slight interruption at the bottom of the valley. A small cingulum crosses the talonid valley. M_2 has weak cingula on the anterior and posterior ends. The anterior cingulum continues internally to the talonid valley, at the opening of which it is slightly notched, and then ceases. A very slight cingulum crosses the valley of the talonid. M_3 has anterior and posterior cingula, weaker, if anything, than those on M_1 and M_2. The anterior cingulum continues internally to the bottom of the trigonid valley and stops. A weak, brief cingulum crosses the talonid valley.

Another left mandibular ramus, M.C.Z. No. 4050, crushed and distorted, with teeth considerably worn and broken, along with isolated teeth, M.C.Z. No. 4052, are referable to *F. whitei*.

TABLE 1
Skull and tooth measurements of *Floridaceras whitei* and *Diceratherium barbouri*

	F. whitei, type M.C.Z. No. 4046		F. whitei, referred M.C.Z. No. 4047		M.C.Z. No. 4048	D. barbouri type M.C.Z. No. 4452
	Right	Left	Right	Left	Right	Right
P^1-M^3	e241.5					
P^2-M^3	e225.0	238.3				
P^{1-4}	e111.3					
P^{2-4}	e 93.7	109.5				
M^{1-3}	140.9	140.6	139.5			c110.0
P^1 AP					23.0	
Tr					19.2	
P^2 AP		e26.3				
Tr		38.2			37.6	
P^3 AP	c34.4	34.5				
Tr	50.3	49.7			41.1	
P^4 AP	39.9	37.3	39.1	38.9		e28.7
Tr	57.0	58.8	c60.7	c60.0	55.2	e40.0
M^1 AP		44.9	42.2	43.7		e34.0
Tr		56.5	62.5			
M^2 AP		48.4	46.4	c46.7		40.2
Tr		61.6	63.2			42.7
M^3 AP		49.7	49.8			c34.8
Tr		56.7	56.4			37.6
Width across zygomata		c324.5				269.5

TABLE 2

Jaw and tooth measurements of *Floridaceras whitei*,
left ramus, paratype, M.C.Z. No. 4435.

Jaw length, symphysis to angle	553.0
Depth, coronoid to ventral border	280.0
Diastema	96.3
P_1-M_3	257.0
P_2-M_3	244.5
P_{1-4}	113.3
P_{2-4}	105.5
M_{1-3}	148.0
P_1 AP	e 9.9 alveolus
P_1 Tr	e 9.9 alveolus
P_2 AP	27.3
P_2 Tr	15.7
P_3 AP	35.6
P_3 Tr	23.0
P_4 AP	37.9
P_4 Tr	26.8
M_1 AP	42.7
M_1 Tr	28.3
M_2 AP	47.2
M_2 Tr	28.3
M_3 AP	58.0
M_3 Tr	27.8
Depth jaw, below P_2	79.6
Depth jaw, below M_2	89.3

A juvenile left mandible, M.C.Z. No. 4051, referable to *F. whitei*, is of particular interest because of the deciduous dentition. The ventral profile of the ramus is slightly bowed. There is a moderate sized alveolus, presumably for dI_2, in the symphyseal region. What is referred to as P_1, discussed earlier, is entirely unworn. It has the protoconid as the main cusp, with the paraconid forming an anterior buttress and with a descending ridge surrounding a small talonid basin. The pattern of dP_{2-4} progressively approaches the molariform level, especially in the asymmetrical talonid crescent. There is typical thin deciduous enamel on dP_{2-4}. A transversely spread protoconid on dP_2 indicates an incipient metaconid; the paraconid is quite distinct and bifurcated anteriorly, incipiently suggesting dP_3; the talonid seems full sized and molariform, which is still more true of dP_{3-4}. The dP_3 has a typical pattern, that is, molariform, except for its great length, and the paraconid region is transversely elongated into a small crescent, which, in this tooth, also has an internal hook

recurved to the rear, partly enclosing the trigonid basin as an inner harbor. The dP_4 is molariform; its thin enamel and its position are the chief proofs it is not M_1. External cingula are notably lacking: P_1 has one on the paraconid but it is barely indicated and highly tenuous on the paraconid of dP_2, and altogether absent on dP_{3-4}. Internal cingula are anterointernal on the paraconid of P_1 with a short continuation anteriorly, from the talonid onto the protoconid; they are absent on dP_{2-4}. The anterior and posterior cingula are poorly developed on the deciduous premolars.

Colbert (1932) described and figured worn lower cheek teeth from the Hawthorn Formation of Florida which he assigned to *Aphelops* sp. As they do not agree too well with *Aphelops, sensu stricto,* but are essentially the same size and agree in such characters as are shown with *Floridaceras whitei,* this genus and species seems a reasonable tentative assignment for Colbert's material.

POSTCRANIAL SKELETON

While the teeth of *Floridaceras whitei,* so far as known, show only average variation, the skeletal elements wherever duplicated show a wider spread in size not related to growth stages. Measurements in tables are arranged in a graduated series so that the unusual variation in a rhinoceros sample of this size becomes apparent at a glance.

The axial skeleton is poorly represented but some information can be distilled out of a few of the better preserved units. The cracked and damaged atlases, M.C.Z. Nos. 7512 and 7513, show that this bone is rhinocerotic, similar to *Trigonias* and *Subhyracodon* but bigger and sturdier. By doubling the measurements of a complete half, the atlas is estimated to measure 340.0 mm. across. The wing is widely expanded and the posteroventral process is blunt but not spiked. There are two axes, M.C.Z. Nos. 7514 and 7515, of which the neural spine forms a heavy keel which broadens posteriorly, presumably to support a heavy head. Neither of the axes are of a size to articulate with the atlases. A robust stubby odontoid process is strongly intruded into the groove in the atlas. A nearly complete anterior thoracic vertebra, M.C.Z. No. 7517, possesses an exceptionally long neural spine, which, although the tip is missing, measures 264.0 mm. anteriorly above the top of the neural canal between the prezygapophyses, and 219.0 mm. posteriorly between the postzygapophyses. A lumbar

vertebra, M.C.Z. No. 7519, shows the transverse process rising slightly toward the tips, and a neural spine that is expanded anteroposteriorly, and also thickened at the tip.

TABLE 3

Measurements of the fore limb of *Floridaceras whitei*

	Element	Length	Width
Scapula	M.C.Z. No. 7467		
	top to front		
	margin of glenoid	445.0	
	top to glenoid	414.0	
Humerus	M.C.Z. No. 7469	425.0	
	M.C.Z. No. 7470	437.0	
	M.C.Z. No. 7468	440.0	
Ulna	M.C.Z. No. 7477		
	segmental[1]	368.0	
	overall	326.0	
Radius	M.C.Z. No. 7474		
	segmental	368.0	
	M.C.Z. No. 7476		
	segmental	378.0	
Carpus	scaphoid to trapezoid	86.4	scaphoid to pisiform
	composite		131.5
Metacarpals			Distal
II	M.C.Z. No. 7494	159.3	45.5
III	missing		
IV	M.C.Z. No. 7495	148.1	45.7
	M.C.Z. No. 7496	159.5	51.4
	M.C.Z. No. 7497	159.7	44.1
	M.C.Z. No. 7498	162.7	51.4
V	M.C.Z. No. 7499	77.3	32.1
	M.C.Z. No. 7500	84.3	29.1
	M.C.Z. No. 7501	85.4	27.3
	M.C.Z. No. 7502	86.7	39.3
	M.C.Z. No. 7503	95.5	31.7
	M.C.Z. No. 7504	95.8	32.8
	M.C.Z. No. 7505	97.1	34.6

[1] Segmental length is measured in the long axis between proximal and distal articular surfaces.

It is interesting to see how well one can picture this remarkable animal in spite of unassociated material. The limb elements about equal the length of those of the black rhinoceros, but are much more slender (Pl. III, fig. 1). The impression persists that it was a very large cursorial beast despite its massiveness. The leg proportions suggest *Trigonias*, or better *Subhyracodon*. There is little similarity to the small slender *Diceratherium cooki* and *Hyracodon* in one direction, and even less to the squat *Teleoceras* in the other, with which it contrasts very sharply. Very few profitable comparisons can be made with any single species as far as limb elements are concerned. The scapula, M.C.Z. No. 7467, is exceedingly long and narrow for an animal of such bulk, but it is also powerful (Fig. 1). There is a fairly close resemblance in outline to that of the Indian rhinoceros. There is no sharp angle between the vertebral and axillary borders, a feature which is so characteristic of rhinoceroses in general. A considerable recurve in the corner between the vertebral and axillary border enlarges the surface for the infraspinatus and especially the teres muscles. The humerus, M.C.Z. Nos. 7468-7472, is like that of *Subhyracodon tridactylus*, much enlarged but stubby. The radius and ulna, M.C.Z. Nos. 7474-7476 and 7477-7483, suggest the equivalents of *Subhyracodon*. They are slender but powerful. These observations indicate that although *Floridaceras* was much bigger, it could run as fast as these lighter weight animals.

The carpus is so complete that it can be reconstructed (Pl. III, fig. 2), lacking only the unciform. This, however, is most unfortunate in that it is impossible to check the articulations with metacarpal V, which is *Floridaceras*' unique character. The carpus was involved in a different weight distribution than in a three-toed manus, is wider than long, with an approximate width across the proximal row of carpals of 131.5 mm., and a length of 86.4 mm., scaphoid to trapezoid. Taken as a functional unit, the carpals compare best with the black rhinoceros but with some dissimilarities in the individual bones in size and modelling. The pisiform resembles that of *Subhyracodon*. The trapezium, a peculiar keeled bone, is unlike rhinoceros trapezia, except in *Aceratherium "gannatense,"* where it appears to agree well with Duvernoy's illustration (1853, pl. VII, fig. 7a). The trapezoid is very large, and the magnum is rather delicate. The carpals as represented are: two left scaphoids, M.C.Z. No. 7485; a left and right lunar, M.C.Z. Nos. 7486 and 7487; a right cuneiform, M.C.Z. No. 7488; two left and one right cuneiforms, M.C.Z. No. 7489; a

Figure 1.   *Floridaceras whitei*. M.C.Z. No. 7467, right scapula. × 1/3.

right pisiform, M.C.Z. No. 7490; a left trapezium, M.C.Z. No. 7491; a left trapezoid, M.C.Z. No. 7492; a right magnum, M.C.Z. No. 7493.

Of the metacarpals, the third and largest is missing. Metacarpals II, M.C.Z. No. 7494, and IV, M.C.Z. Nos. 7495-7498, are generally like those of the black rhinoceros, but the proximal end of metacarpal IV resembles that of the white rhinoceros. All of the fourth metacarpals bear a proximal lateral facet for metacarpal V and make a good fit with the corresponding metacarpal V (Pl. III, fig. 2). The second and fourth metacarpals are very similar in size and proportions and even details of structure to those of the fragmentary *Aphelops longipes* (Leidy and Lucas, 1896, pl. 13, figs. 6 and 7) from the Pliocene Alachua Formation of Florida. This resemblance is the closest I have observed, whether in fossil or living rhinoceroses, and together with the geographic location, suggests the possibility of direct descent from *Floridaceras*, in which case *A. longipes* could not be an *Aphelops;* the teeth assigned to *A. longipes* are larger and more advanced.

A remarkable and at first puzzling bone has proved to be metacarpal V of a complete, though relatively short functional digit (Pl. IV, fig. 2a-d). This bone was so unexpected and peculiar as to have suggested the possibilities of other families and even orders. Far-fetched assignments such as chalicothere, big carnivore, *Teleoceras* and even proboscidian were considered and ruled out. It was eliminated from other members of the Thomas Farm fauna on the basis of either size or character or both. Since there are seven complete examples of this metacarpal, and one damaged, M.C.Z. Nos. 7499 - 7506, all alike, it is not an anomaly and therefore must belong to a known member of the fauna. Its size would fit only *Floridaceras,* and yet an early Miocene form with a fifth digit has never been discovered in an American true rhinoceros line. The bone shows obvious resemblances to a tapir metacarpal V, and still more to various extinct tetradactyl rhinoceroses. The Thomas Farm metacarpal V (Pl. IV, fig. 2) has a double proximal facet, forming a right angle, rounded off at the apex, on its proximal and posterior surfaces to articulate with the unciform. There is a hint of this unusual character in metacarpal V of modern tapirs (Kaup, 1859, pl. II, figs. 2 and 2a; A.M.N.H. No. 2592) and in *Protapirus* (A.M.N.H. No. 662; Wortman and Earle, 1893, fig. 4; and Scott, 1941, pl. LXXX, fig. 2). It is better matched, among rhinoceroses, in the fifth metacarpals of *Hyrachyus affinis,* A.M.N.H. No. 12664, in *Aceratherium lemanense* (Duvernoy, 1853, pl. VII, figs. 14a, 14a′,

14a ′ ′ ′, *A. "gannatense")*, and apparently in *A. depereti* (Boris-siak, 1927, pl. 2, fig. 5), and even in the metacarpal V, a mere nubbin, in the white rhinoceros, A.M.N.H. No. 51862.

There are general resemblances between this metacarpal and the unmodified, more primitive metacarpal V of *Trigonias*, shown in the specimens, *T. osborni*, A.M.N.H. No. 9847 (cf. Hatcher, 1901, pl. III; Scott, 1941, pl. LXXXIII, fig. 7), in *T. wellsi*, A.M.N.H. No. 13226C, and in *T.* cf. *gregoryi*, A.M.N.H. No. 13226D (Pl. IV, fig. 1a-d). Finally, the *Floridaceras* bone virtually duplicates in all respects, including size, the metacarpal V of *Aceratherium incisivum* described and figured by Kaup (1834, p. 58, pl. XV, fig. 4; 1859, pp. 163-167, pl. II, figs. 1, 1a, and 4). This resemblance is so close that Kaup's fine illustrations could readily represent M.C.Z. No. 7499 in every respect except the shape of the inner proximal facet for metacarpal IV! Kaup (1834, p. 58) states that this bone was associated with other bones of *A. incisivum*, including a fragment of lower jaw with teeth. He gives the measurements as 80.0 mm. long, 15.0 mm. wide at the proximal articulation and 33.0 mm. at the distal facet, which agrees well with his 1859 illustrations, of which his figures 1 and 1a, although not so stated, are about natural size. These measurements fit neatly into those for the Thomas Farm metacarpal V (see Table 3). The double proximal facet calls for a corresponding concave external distal articular facet on the unciform as is the case in the tapir and white rhinoceros. Since no unciform has come to light in the Florida material, only approximate fits can be made with modern African rhinoceroses.

The transversely narrow proximal end of metacarpal V resembles *Trigonias* (cf. Pl. IV, figs. 1b, 2b), *Aceratherium lemanense*, and, even more exactly, *Aceratherium incisivum*. The ventral 70° bend of the shaft (Pl. IV, fig. 2a,c) is much more extreme than that of *Trigonias* in which it is only 30°. This bend is closer to that of *Aceratherium lemanense* and agrees exactly with *A. incisivum* (Kaup, 1859, pl. II). The significance of this bend is that it permitted the digit to touch the ground, bending over the elastic pad which gives the rhinoceros its characteristic bouncy gait. The heavy rugosities at muscle insertions suggest active use. The foot appears to have been somewhat splayed, perhaps associated with a soft or marshy ground habitat. The bulbous distal ends compare respectably in size with those of metacarpal IV and give the impression of being swollen, with a recess of varying size on the medial surface, just proximal to the trochlea. The trochlea is large and markedly asymmetrical; it is even more on

the bias than the distal end, in general, which is broadly comparable to that of *Trigonias* or even of *Metamynodon*. Although no phalanges can be assigned to this digit, the swollen distal end and large trochlea make it certain that the toe was complete (Pl. IV, figs. 1b, 2b), and most probable that it touched the ground however shortened it may have been.

In the posterior limb, the big ilium, M.C.Z. No. 4053-I, is broadly comparable with *Subhyracodon* (Peterson, 1920, fig. 34) but has a more widely expanded blade; it is less excavated anterior to the acetabulum. A right and a left femur, M.C.Z. Nos. 7524 and 7525, are mashed flat, exaggerating the genuine effect of long legs. Surprisingly enough, the closest match among rhinoceros femora is to the elongated femur of *Metamynodon*, though *Floridaceras* lacks the extreme flattening of the former. A scale enlargement of *Diceratherium cooki* would be the next best comparison of the femur. The tibia (M.C.Z. Nos. 7527-7533) is sturdy but slender, suggesting particularly an enlargement of *Subhyracodon tridactylus*. The fibula (M.C.Z. Nos. 7534-7536) is unusually long and slender, differing from most rhinoceroses, but having similarities of proportions to those of *Hyrachyus* and *Hyracodon*.

The pes, not as well represented as the manus, is big and generalized. The tarsals are suggestive of the black rhinoceros but are somewhat smaller. They are stouter and coarser than *Subhyracodon* but also somewhat shorter, relatively. The *Floridaceras* material has large calcanea and astragali, but not as large as in *Trigonias wellsi*. Smaller specimens are close in size to those of *T. gregoryi*, but all have more delicate modelling and a longer tuber calcis. The *Floridaceras* tarsus as a whole is neither squat nor exceptionally long. The calcanea are heavy and coarsely modelled as in the black rhinoceros, but the plantar process is shorter and blunter. It is blunter than that in *T.* cf. *wellsi*, *T.* cf. *gregoryi*, *Subhyracodon occidentalis* and *Diceratherium* cf. *annectens*. The naviculars (M.C.Z. No. 7542) are broadly similar to those in rhinoceroses of the same size. A left ectocuneiform (M.C.Z. No. 7545), resembles that of the white rhinoceros in proportions.

The three metatarsals are represented, and while resembling those of the two living African rhinoceroses, do not agree exactly with either. Metatarsal II (M.C.Z. Nos. 7547 - 7549) is noticeably shorter and stouter than the corresponding bone of *Trigonias wellsi* and *gregoryi* though *Floridaceras* was the larger animal. Two of the three specimens of metatarsal II show no facet for

the entocuneiform, which was therefore either much reduced, or more probably, somewhat everted. M.C.Z. No. 7549 bears what appears to be a small facet for the entocuneiform in a somewhat more lateral position than usual. Metatarsal III (M.C.Z. Nos. 7550 - 7552), by far the predominant digit, is essentially bilaterally symmetrical in anterior aspect, and is markedly broader than the lateral metatarsals.

There is an assortment of sesamoids and phalanges in the collection which offer nothing constructive. For what little it is worth, a composite of the phalanges of a lateral digit, attributed to the manus, M.C.Z. No. 7511, measures 79.1 mm. in length.

Table 4

Measurements of the hind limb of *Floridaceras whitei*

Element		Length	Width
Ilium	M.C.Z. No. 4053	384.0 in front of acetabular rim	466.0
Femur	M.C.Z. No. 7524	580.0 segmental	
Tibia	M.C.Z. No. 7532	337.0 segmental 375.0 overall	
Fibula	M.C.Z. No. 7534	382.0	
Tarsus	astragalus and cuboid composites	112.0 118.0	calcaneum and astragalus composite 105.7
			depth of same 83.2

Metatarsals			Proximal	Distal
II	M.C.Z. No. 7548	137.7	35.5	41.1
	M.C.Z. No. 7547	148.8	34.0	41.2
	M.C.Z. No. 7549	149.0	36.6	42.2
III	M.C.Z. No. 7550	153.5	56.4	61.5
	M.C.Z. No. 7552	155.6	51.7	58.1
	M.C.Z. No. 7551	168.5	53.6	54.8
IV	M.C.Z. No. 7555	141.4	44.5	39.2
	M.C.Z. No. 7556	142.3	45.1	40.1
	M.C.Z. No. 7554	142.3	46.1	38.7
	M.C.Z. No. 7553	144.7	43.4	35.3

Genus DICERATHERIUM Marsh, 1875
Subgenus MENOCERAS Troxell, 1921

Subgeneric diagnosis: Conforming broadly to the *Diceratherium* pattern; relatively small, slender and long legged; especially prominent paired round knobs on nasals, assumed to be horn supports in males, absent or weakly developed in females; posterior bend of zygomatic arch sharp, essentially a right angle; ectolophs of upper cheek teeth elongated, so as to appear sub-hypsodont; in correlation, buccal pits and sinuses tend to be deep; strong development of cristae, and especially of crochets.

DICERATHERIUM (MENOCERAS) BARBOURI [1] new species

Type: M.C.Z. No. 4452, a palate, *basis cranii* and occiput.

Hypodigm: The type and M.C.Z. Nos. 4061, 7441-7466, 9328-9329, teeth and isolated bones representing most parts of the skeleton.

Horizon and locality: Thomas Farm local fauna, late Arikareean, eight miles north of Bell, Gilchrist County, Florida.

Diagnosis: Slender, long-legged form, more cursorial than any living rhinoceros, proportions and approximate size of *D. cooki*, but having somewhat longer legs; huge, elongated postglenoid process, completely overshadowing paroccipital process; ectolophs of cheek teeth higher crowned than *D. cooki;* median valleys very deep, close to ectolophs; large sharp crochets with corrugated margins; sharp narrow cristae, protolophs smooth, simple and uncomplicated; internal cusps low; protocones not markedly pinched off; M^2 disproportionately elongated anteroposteriorly.

DISCUSSION

Diceratherium(Menoceras) barbouri shows close resemblance only to *Diceratherium cooki,* among other rhinoceroses. It is a little larger and somewhat longer limbed cursorial form. The cheek teeth have slightly higher crowns and a little more complicated pattern. These differences are such as might reasonably occur in a direct descendant of *D. cooki* found in beds of slightly younger age. Interestingly enough, I received almost precisely similar isolated upper teeth from a local collector, sent me from near Bridgeport, Nebraska, presumably from the Marsland. The

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[1] The specific name is given in recognition of the late Dr. Thomas Barbour.

dentition of *Diceratherium barbouri* shows some few resemblances to that of *Floridaceras whitei* from the same quarry, presumably reflecting partial parallelism. In other respects the two forms are widely different and non-competing. Since the *Diceratherium* line has left no known descendants beyond *barbouri*, it is plausible that the *Parahippus-Merychippus* line eliminated it from the competition just as *Miohippus* perhaps crowded out *Hyracodon* at the end of the Oligocene.

CRANIUM

The type of *D. barbouri*, M.C.Z. No. 4452, a palate, *basis cranii* and occiput is damaged so that only a limited number of cranial characters can be determined. The greatest width across the zygomatic arches, 269.5 mm., is not seriously distorted and it is probably of the right order of magnitude. Posteriorly, the zygomatic arches bend sharply, much as in *D. cooki*. The postglenoid and posttympanic processes, now shoved together, were not fused or appressed, but were probably in contact or thereabouts. A striking character is the huge size and extreme projection of the postglenoid process beyond the glenoid fossa: it projects 89.1 mm. on the right side, and 72.3 mm. on the left, well beyond the corresponding paroccipital processes (80.3 mm. and 54.2 mm.), which are of typical size. Whatever crushing has taken place would tend to reduce these measurements rather than to increase them. The postglenoid process is directed mostly ventrally, somewhat medially, and curves anteriorly at the tip. It also markedly exceeds the length of the well developed postglenoid process of *D. cooki* (35.7 mm.—44.2 mm.), an animal of the same general size.

The measurements of the postglenoids of three *D. cooki* skulls, A.M.N.H. Nos. 14236, 16B (field number), and 14213, gave respectively 35.7 mm., 35.8 mm., and 44.2 mm., as against 74.1 mm. for the same process in *D. barbouri*. Even rhinoceroses with unusually large postglenoid processes, such as *Ceratotherium*, *Peraceras*, *Teleoceras*, and especially *Aphelops mutilus,* do not have processes which equal the exaggerated proportions in *D. barbouri*. The sagittal contour line of the occiput is a simple slightly concave curve, as is usually the case in *D. cooki,* instead of the sine curve which is typical of many rhinoceros skulls.

DENTITION

The teeth present in the type skull, M.C.Z. No. 4452, consist of P^4 - M^3 of both sides, and are damaged in varying degrees. The

ectolophs are higher than in *D. cooki*, whether viewed laterally or measured from the external deep point of the median valley; there is no corresponding tendency toward hypsodonty in the lingual portion of the teeth. The anteroposterior (mesio-distal) dimension of M^2 is unusually long in proportion to the transverse measurement (Pl. 5). The crochets of P^4 - M^2 are a striking feature; they are unusually long and sharp, with accessory vertical ridges which give a corrugated appearance to the sides of the crochet. Some individuals of *D. cooki* show approaches to this type of crochet in one or more teeth. The crochet of M^3 is a small sharp blade. The cristae of M^{2-3} were sharp blades when unworn, and seem to have been sharp also on P^4 - M^1. The protolophs are smooth and simple, without antecrochets on P^4 and M^{2-3}, and with only a small one on M^1. The protocones are only slightly pinched off: there is a definite anterior groove on M^1, as well as a faint anterior groove on M^2; otherwise the protocones are entirely confluent with the rest of the protolophs. The internal cingula are complete on P^4 - M^3. Altogether, these teeth suggest an exaggeration of the characters of *D. cooki*, such as might be expected in a descendant. The collection of teeth sent to me from Nebraska shows, by all odds, the closest resemblance to *D. barbouri*.

There are fragmentary miscellaneous lower teeth. A right I_2, M.C.Z. No. 7443, has the characteristic shape of the lower tusk (Pl. V, fig. 6); it is generally slender, and well worn at the tip. It might have once had a longer crown than is typical of *D. cooki*. There are right (Pl. V, fig. 3) and left examples of P_2, M.C.Z. No. 7444: they have strong external and internal cingula, and a deep groove buccally, delimiting the talonid from the trigonid. A group of loose broken lower cheek teeth (M.C.Z. No. 7445) suggests fragments from one dentition. The larger pieces include the hypoconid of M_1, most of the external part of M_2, and an entire M_3, with the trigonid crescent slightly worn. This M_3 is generally comparable to corresponding teeth of *D. cooki*, but is somewhat higher crowned (Pl. V, figs. 4, 5).

AXIAL SKELETON

The few vertebrae assignable to *D. barbouri* include an atlas (M.C.Z. No. 4061) and an axis (M.C.Z. No. 7441). The atlas is complete and essentially uncrushed; it is a little larger than in *D. cooki*, measuring 177.0 mm. as opposed to 160.0 mm.

APPENDICULAR SKELETON

A fair number of limb elements are preserved and show that the legs were long and slender. This impression of length characterizes the scapula, M.C.Z. No. 7447, the ulna, M.C.Z. No. 7448, metacarpal III, M.C.Z. No. 7449, the femur, M.C.Z. No. 7450, the fibula, M.C.Z. No. 7451, and metatarsal IV, M.C.Z. No. 7452. The scapula is like that of *D. cooki* with some similarity to *Subhyracodon.*

The only carpals are a left lunar, M.C.Z. No. 7453 and a right pisiform, M.C.Z. No. 7454, both resembling *D. cooki*, with the differences that the lunar is stouter and the pisiform has less neck. Right metacarpal III, M.C.Z. No. 7449, resembles *D. cooki,* but is considerably larger. The bone is crushed but it is clearly longer and stouter. A left metacarpal IV, M.C.Z. No. 7455, agrees closely with *D. cooki,* but is a shorter bone. Comparison with the same bone in *Floridaceras* is striking; the metacarpal IV of *D. barbouri* is 72 per cent as long, but only half of any transverse measurement. A number of phalanges are similar to *D. cooki,* but are a little stouter and more rugose.

Figure 2.   *Diceratherium barbouri.* M.C.Z No. 7456, left half of pelvis. *A,* dorsolateral; *B,* lateral. × ¼.

Enough of the pelvis and hind limb is present to make further comparisons with *D. cooki.* The pelvis, M.C.Z. 7456, is too fragmentary for reliable measurement: what there is of it is small and delicate (Fig. 2). A shaft and distal end of a femur, M.C.Z. No.

7450, is close in character to *D. cooki,* but is proportionately long-
er. The shaft is just about the same diameter as that in *Subhyraco-
don occidentalis* but was undoubtedly much longer. The preserved
length is 366.0 mm., with an estimate of 390.0 mm. for the whole
femur. A left fibula, M.C.Z. No. 7451, measuring 250.0 mm., gives
an indication of the length and slenderness of the shank.

The tarsals, a right astragalus, M.C.Z. No. 7457, a left calcan-
eum, M.C.Z. No. 7458, and a left entocuneiform, M.C.Z. No. 7459,
are close to *D. cooki.* The calcaneum and entocuneiform are stout-
er than in *D. cooki,* and the astragalus is quite noticeably more so.

Like the metacarpals, the metatarsals resemble the correspond-
ing bones of *D. cooki,* but are sturdier. Metatarsals III and IV,
and fragments of metatarsal II bear this out (M.C.Z. No. 7452).

TABLE 5

Comparative measurements of *D. barbouri* and *D. cooki.*
Measurements of *D. cooki* from Peterson, 1920.

Element	*Diceratherium barbouri*			*Diceratherium cooki*	
Atlas	M.C.Z. No. 4061	177.0 overall		160.0	
		67.8 condyles			
		Length	Width	Length	Width
Scapula	M.C.Z. No. 7447	301.0 overall		273.0	138.0
		282.0 segmental			
Humerus	M.C.Z. No. 7461	293.5 overall		250.0	
		c273.0 segmental			
Radius	M.C.Z. No. 9328	c232.0		250.0	
Ulna	M.C.Z. No. 7448	300.0 overall		315.0	
		232.0 segmental			
Mc. III	M.C.Z. No. 7449	156.5	37.6 distal	138.0	
			37.9 proximal		
Mc. IV	M.C.Z. No. 7455	115.4		115.0	
	M.C.Z. No. 9329	130.0			
Femur	M.C.Z. No. 7450	c390.0		323.0	
Fibula	M.C.Z. No. 7451	250.0			
Mt. II				110.0	
				126.1 A.M.N.H.	
Mt. III	M.C.Z. No. 7452	c140.0		125.0	
Mt. IV	M.C.Z. No. 7452	130.3		110.0	
				116.5 A.M.N.H.	

CORRELATION AND PALEOGEOGRAPHY

White (1942) apparently regards the Thomas Farm local fauna
as a unitary one, representing an essentially contemporaneous as-
semblage. This is a reasonable interpretation of the evidence, how-
ever convenient it might be to split the fossils between two, or even

more, faunas of different ages, thereby resolving contradictory in-
dications. He places the Thomas Farm local fauna earlier, in terms
of the North American continental scale, than had previously been
suggested, considering it as early Lower Miocene (lower Arikar-
eean). The rhinoceroses do not confirm this assignment, and offer
some evidence to the contrary. In stage of evolution, without im-
plication of special relationship, the check teeth of *Floridaceras*
are reminiscent of *Diceratherium armatum* of the John Day, but
are somewhat more advanced. The limbs are strikingly long
legged, agreeing in this only with *"Aphelops longipes"* of the
Mixon bone beds (Alachua fauna) now considered Hemphillian
(Middle Pliocene). *Diceratherium barbouri* is a sturdier and more
advanced version of *D. cooki,* but is small and slender compared
with *F. whitei,* or, for that matter, with most true rhinoceroses. In
view of its evolutionary isolation, *Floridaceras whitei* has no pre-
cise value in correlation, but is more probably Lower Miocene than
either earlier or later. *Diceratherium barbouri,* as a species some-
what more advanced over *D. cooki,* indicates post-Harrison time,
i.e., latest Arikareean or possibly earliest Hemingfordian. This
agrees with the consensus as to the Thomas Farm local fauna.

I believe that White (1942) attaches too much significance to
his phyletic inferences from paleogeographic considerations, and
hence his correlation is biased by these considerations. There is no
reason to suppose that the Okefenokee Trough was ever more than
a shallow trough. Assuming that the former existence of a strait
separating a Florida island from the mainland is demonstrated,
comparable existing analogies would be with England, Ireland,
Newfoundland, or the Behring Straits, rather than with Cuba or
Madagascar. Japan, Borneo, Java and even Sumatra are more cut
off structurally from the Asiatic mainland than was the "Florida
island," yet their faunas do not show the long history of localized
evolution inferred by White for Florida but are close to that of the
mainland. He believes that intermittent connection by oscillation,
bars, etc., can be virtually excluded for a long period of time; but
this seems to go far beyond what may be inferred with any confi-
dence from the absence of data. Compare the cases cited above and
also dubious evidence cited by White (1942, pp. 36, 37, 41 and 42).
Where the peculiar elements in the fauna can represent climatic or
other facies differences, the resemblances to Great Plains and
Texas faunas are of more significance in correlation than the forms
peculiar to the Florida fauna. Bader (1956, p. 70) comes to a sim-
ilar conclusion in his analysis of the Thomas Farm horse fauna.

White's conclusion as to the fundamental geographic separation

of the Florida island fauna from the mainland leads him to the *a priori* improbable hypothesis (1942, p. 42 and implied elsewhere) that a small, isolated southern outlier of the continent gradually developed stock which later invaded the continent when connection was reestablished, and became a considerable element in the later Miocene of the mainland against competition from the pick of a vastly larger area. With all deference to White's special knowledge, I should prefer a more conservative view of the age of this fauna, putting it close to the Arikareean-Hemingfordian boundary. Further evidence could easily shift its position a little, either way. I should also postulate a less complete, perhaps intermittent isolation with elderly phyletic lines surviving in the mild Florida climate, along with bustling northern visitors, so that the latter would give a more dependable check on correlation with the standard sequence. The correlation of mammal-bearing marginal, littoral or marine deposits with the main continental sequence is extremely important; there is no intention to suggest that a definitive correlation has already been reached (whether in Wood, *et al.*, 1941 or elsewhere). If such an idea were entertained, the Quitman, Mississippi, titanothere (Gazin and Sullivan, 1942) would prove the contrary. So detailed a critique is offered because the Thomas Farm local fauna is the most important assemblage of Tertiary land mammals which has yet been discovered in eastern North America.

SUMMARY

1. The Thomas Farm local fauna has yielded two cursorial caenopine rhinoceroses. One is enormous, the other small and delicate.
2. *Floridaceras whitei*, the larger form, dwarfs all its New World contemporaries. It is advanced over Oligocene and Arikareean rhinoceroses, but it is primitive and unmodified compared with Hemingfordian forms and still more so, with later rhinoceroses.
3. *F. whitei* has a tetradactyl manus with a functional fifth digit. This character establishes a distinct line of ancestry back to, say, the early Oligocene *Trigonias*. In view of this evolutionary isolation, it has limited correlative value, but the most reasonable assignment is Lower Miocene.
4. *Diceratherium barbouri*, the smaller form, is slightly more advanced than *D. cooki*, its presumed ancestor. It extends this line, from which there had been no previously reported descendant. Since *D. barbouri* is progressive over the classic

Lower Miocene index fossil, *D. cooki,* it indicates post-Harrison time, i.e., latest Arikareean or possibly earliest Hemingfordian. This agrees with the consensus as to the age of the Thomas Farm local fauna.

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